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## RELATIONSHIPS OF HESPEROLINON AND LINUM (LINACEAE)

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*Hesperolinon* is a genus of about a dozen closely related annuals, restricted mainly to serpentine soils of the North and South Coast Ranges of California. It was at first treated as a section of *Linum* (Gray, 1865) and later elevated to a genus (Small, 1907), a status upheld by Sharsmith (1961) who described *Hesperolinon* in some detail. At the same time, it is clearly related to *Linum* and its narrow geographical and ecological range, little morphological diversity, and rather high degree of specialization when compared to the large, diverse, and worldwide *Linum* suggest that *Hesperolinon* may be an evolutionary segregate of that genus.

A comparison of *Hesperolinon* with various species of *Linum*, as well as with other genera, reveals that it is among species of *Linum* sect. *Linastrum* that the most similar species are found. Sharsmith (1961, p. 273), after comparing *Hesperolinon* with species of several sections of *Linum*, concluded that "*Linum*, section *Cathartolinum* [*Linastrum*] (North American species only), in many ways bridges the morphological hiatus between the rest of *Linum* and *Hesperolinon*. There appears to be a stabilization in *Hesperolinon* of many of the tendencies found incipiently in *Linum* section *Cathartolinum* [*Linastrum*]."

A survey of the relationships of the approximately forty North American taxa of sect. *Linastrum* (Rogers, 1963, 1968, 1969) showed that they comprise five distinct "complexes". Some conclusions were also reached with regard to which species are primitive and which are specialized for several variable features in these North American species. A number of the characteristics that distinguish *Hesperolinon* from *Linum* appear to be further specializations of these. When these features and their distribution among the five complexes are compared with those possessed by *Hesperolinon*, it is possible to place these groups in a tentative evolutionary arrangement (fig. 1). Brief descriptions of these characters will help clarify how each has helped in interpreting relationships.

**STAMINODIA.** Diminutive structures alternating with the stamens have generally been interpreted as staminodia. They are found more or less throughout *Linum* and their absence is considered a specialization. In North American sect. *Linastrum* they are found only in the primitive *L. schiedeanum* complex. They are also absent in *Hesperolinon*.

**LEAF ARRANGEMENT.** It was concluded (Rogers, 1969), on the basis of its close correlation with other features considered primitive among North American species of sect. *Linastrum*, that whorled basal leaves are primitive in this group. Evolution to opposite and alternate leaves has probably taken place several separate times and most of the North American species have opposite or alternate leaves. Only in the *L. schiedeanum* complex and in *Hesperolinon* are leaves in whorls.

**STIPULAR GLANDS.** These structures are widespread in *Linum* and are uniformly present among North American species thought to be primitive. Their loss has clearly occurred in other sections of the genus as it has in the *L. virginianum* and *L. neomexicanum* complexes and a few species of the *L. rigidum* complex of sect. *Linastrum*. *Hesperolinon* species have retained this "primitive" character although the glands are commonly poorly developed.

**FALSE SEPTA.** The intrusion of false septa makes the fruit of *Linum* more or less ten-celled. Partially developed false septa are characteristic of most of the genus. Most of the *L. rigidum* complex and two or three species in the *L. virginianum* complex have complete or essentially complete false septa and are considered specialized with respect to this character. *Hesperolinon* is similar to other species of *Linum* in having incomplete false septa.

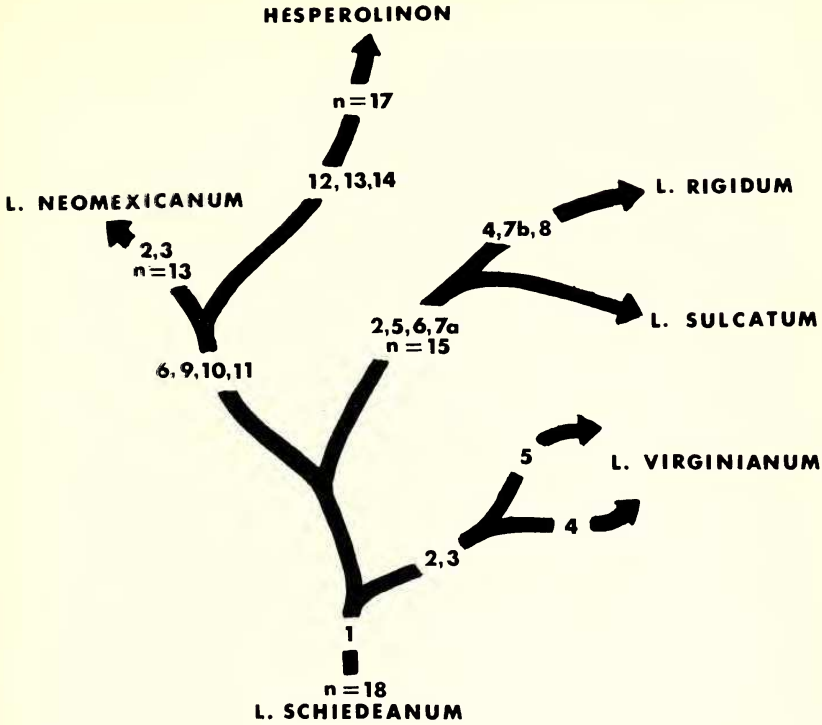


FIG. 1. Evolutionary relationships of five "complexes" of North American species of *Linum* sect. *Linastrum* and *Hesperolinon*. Changes in chromosome number are indicated; other numbers refer to the following: 1, loss of staminodia; 2, whorled → opposite or alternate leaves; 3, loss of stipular glands; 4, partially developed → completely developed false septa; 5, tricolpate → multiporate pollen; 6, perennial → some or all annual; 7a, separate → basally united styles; 7b, styles completely united or nearly so; 8, twice as many → same number of fruit segments as carpels; 9, acquisition of petal auricles; 10, acquisition of non-yellow corollas; 11, petal attachment at or near base → summit of stamen tube; 12, acquisition of conspicuous petal appendages; 13, five → three/two carpels and styles; 14, lens-shaped → wedge-shaped seeds in cross-section.

**POLLEN MORPHOLOGY.** The "basic" pollen grain in *Linum* is tricolpate, although multiporate pollen has evolved several times in the genus (Rogers and Xavier, 1972), including the *L. sulcatum* and *L. rigidum* complexes and some species of the *L. virginianum* complex. *Hesperolinon* has retained tricolpate pollen. Xavier (1967, p. 32) noted, "The pollen of the genus *Hesperolinon* resembles that of some species of the *Pringlei-neomexicanum* group and to the *Digynum* type. Similarity in pollen morphology and closeness of geographic distribution support the relationship between the *Pringlei-neomexicanum* group, *Digynum* and the *Hesperolinon* group."

LONGEVITY. Almost all species of *Linum* are herbaceous. Perennials are generally considered more primitive than annuals. Annual species are found scattered throughout the genus. A number of North American species, principally the *L. sulcatum* and *L. rigidum* complexes, plus *L. neomexicanum* are annuals. All species of *Hesperolinon* are also annuals, although their comparative diminutiveness and delicateness tend to distinguish them qualitatively from *Linum*.

UNION OF STYLES. The five styles in *Linum* are usually separate. *Linum sulcatum* has partially united styles, while species of the *L. rigidum* complex are characterized by styles united nearly to the summit. *Hesperolinon* resembles more primitive species in having separate styles.

FRUIT DEHISCENCE. Fruit of *Linum* and *Hesperolinon* separate into twice as many one-seeded segments as carpels, except fruits of the *L. rigidum* complex, which are unique in the genus in splitting loculicidally into five two-seeded segments.

PETAL AURICLES. Auricles at the base of the petals are generally present in *Hesperolinon* and have been cited as one of the generic characters. As Sharsmith noted, however, these are equally prominent in a few species of *Linum*. These prove to be the taxa that comprise the *L. neomexicanum* complex.

PETAL PIGMENTATION. With the exception of the white-flowered *L. pringlei* of the *L. neomexicanum* complex, sect. *Linastrum* is characterized by yellow flowers. *Hesperolinon* is about equally divided between white- and yellow-flowered species. A comparison of floral pigments among North American species of sect. *Linastrum* proved to be of considerable value in assessing relationships (Giannasi and Rogers, 1970). Giannasi has made some initial studies of the floral pigments of *Hesperolinon* and makes the following statement (pers. comm.): "a number of compounds found in *Hesperolinon* may also be observed in *Linum*: specifically in the *L. schiedeianum* and *L. neomexicanum* taxa, rather than the *L. rigidum* taxa." Apigenin-c-glycoside, characteristic of all five of the *Hesperolinon* species tested (including both white- and yellow-flowered species), was found otherwise only in species of the *L. neomexicanum* complex.

PETAL ATTACHMENT. One of the features that Sharsmith (1961) stressed as helping to set *Hesperolinon* apart from *Linum* is the attachment point of the petals, which in *Hesperolinon* is at the summit of the stamen tube in the usual position of the staminodia. In most species of *Linum* they are attached at or near the base of the stamen tube. It is very likely significant, therefore, that the few exceptional species of *Linum* that have petals in this unusual position are those of the *L. neomexicanum* complex.

PETAL APPENDAGES. These consist of "horizontal crests" located near the auricles and a central appendage on the midvein near the base of the petal. These are commonly well developed in *Hesperolinon* and served as the principal feature upon which Small (1907) removed these species

from *Linum*. They are apparently present, although less developed, in *Linum* as well. Sharsmith (1961) mentioned species of the *L. rigidum* and *L. neomexicanum* complexes particularly, so although their prominence in *Hesperolinon* is a reasonable generic character, they seem to be best interpreted as a further elaboration of structures already present in species of sect. *Linastrum*, to some extent even among the species considered primitive.

**STYLE AND CARPEL NUMBER.** The entire genus *Linum* is characterized by five-carpellate fruits. Perhaps the most significant constant difference between *Linum* and *Hesperolinon* is that the latter has three- or two-carpellate fruits.

**SEED SHAPE.** Seeds of *Linum* are uniformly lens-shaped in cross-section, while those of *Hesperolinon* are narrowly triangular or wedge-shaped in cross-section. Seed shape is correlated with and may in fact be an effect of the reduced carpel number but does constitute an additional generic difference. *Sclerolinon digynum*, another species of far western United States, also has wedge-shaped seeds in two carpellate fruits. It is surely related to both *Hesperolinon* and *Linum*, although many basic dissimilarities preclude its being on a direct evolutionary line involving *Linum* and *Hesperolinon* (Rogers, 1966).

**CHROMOSOME NUMBER.** Chromosome numbers have been established for most of the North American taxa of *Linum* and *Hesperolinon*. The primitive number in the North American species of the sect. *Linastrum* appears to be  $n = 18$  (Harris, 1968). It is characteristic of the *L. schiedeanum* and *L. virginianum* complexes, while the *L. sulcatum* and *L. rigidum* complexes, with  $n = 15$ , and the *L. neomexicanum*, with  $n = 13$ , are thought to be aneuploid derivatives. Of the eleven species of *Hesperolinon* for which chromosome numbers are known, seven have  $n = 18$  and four have  $n = 17$ . The lower number is to a degree correlated with reduction of carpel number from three to two (Rogers et al., 1972).

**GEOGRAPHICAL DISTRIBUTION.** Although it is clear that distributions at the time the diversification into *Hesperolinon* and the various complexes of *Linum* was taking place may have been quite different from the present ones, the close resemblance of *Hesperolinon* to North American species rather than to those of other parts of the world is significant. Within the North American sect. *Linastrum*, the *L. rigidum* and *L. neomexicanum* complexes are geographically nearest to *Hesperolinon*, although none overlaps the range of *Hesperolinon*.

#### CONCLUSIONS

On the basis of interpretations presented here, it is possible to draw conclusions about evolutionary relationships among North American complexes of *Linum* sect. *Linastrum* and *Hesperolinon*. Species of the *L. schiedeanum* complex, as noted earlier, are thought to possess the greatest number of primitive features. The *L. virginianum*, *L. sulcatum*, *L. rigidum*, and *L. neomexicanum* complexes each have traits that set

them apart from a possible evolutionary line leading from *L. schiedeanum* to *Hesperolinon*. The *L. virginianum* complex, although differing from species of the *L. schiedeanum* complex in only a few characteristics, is best interpreted as constituting a small evolutionary side branch of closely related eastern North American species. The *L. sulcatum* and *L. rigidum* complexes, because of their similarity in chromosome number, united styles, and unique multiporate pollen, are thought to constitute another line of evolution, culminating in some of the most highly specialized species in the genus. While the *L. neomexicanum* complex is also a specialized group with a unique chromosome complement, most of the features that make it unique in *Linum* are ones in which it resembles *Hesperolinon*. *Hesperolinon* can be described as having a combination of the primitive features found in the *L. schiedeanum* complex and of traits found in the *L. neomexicanum* complex. Excluding the few generic traits unique to it, *Hesperolinon* possesses no features that are not found in the *L. schiedeanum* or *L. neomexicanum* complex or both.

Postulated relationships are shown in Figure 1. The hypothetical "common ancestor" to *Linum* and *Hesperolinon*, located at the juncture at which *L. neomexicanum* branches off the line leading from *L. schiedeanum* to *Hesperolinon*, would be characterized by features retained from its *L. schiedeanum* ancestor (whorled leaves, stipular glands, partially developed false septa, tricolpate pollen, separate styles, dehiscence of fruit into twice as many segments as carpels, seeds lens-shaped in cross-section, and chromosome number of  $n = 18$ ), together with features that *L. neomexicanum* shares (absence of staminodia, annual habit, presence of petal auricles, white as well as yellow flowers, and petals attached at the summit of the stamen tube). The reduction of carpel number and concomitant alteration of seed shape and the elaboration of petal appendages are the principal morphological features that set *Hesperolinon* apart from this common ancestor. Its geographical and ecological isolation from closely related species may also be significant. *Hesperolinon* is clearly not separated from *Linum* by a great array of characters. There is, however, a distinct gap between it and species of the *L. neomexicanum* complex, which appears to include its nearest relatives.

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DISTRIBUTIONAL AND ECOLOGICAL NOTES ON *PINUS CULMINICOLA*.—Until recently, Potosí piñon or *pino enano* in Spanish vernacular, *Pinus culminicola* Andresen & Beaman, a high altitude dwarf piñon, was known only from the summit of Cerro Potosí (ca 3600 m) in Nuevo León (24° 53' 30" N, 100° 10' 30" W) where it was thought to be endemic (Andresen and Beaman, J. Arnold Arbor. 42:437-441, 1961; Beaman and Andresen, Amer. Midl. Naturalist 75:1-33, 1966). However, in 1972, Capó-Arteaga in an unpublished thesis (*Observaciones sobre la taxonomía y distribución de las coníferas de Nuevo León, Mexico*. Tesis, Fac. Ciencias Biol., Univ. Nuevo León, Monterrey, N.L.) and again in a popular Mexican forestry journal (Bosques 9:33, 1972) mentions that he collected the Potosí piñon from the Sierra de la Marta in Nuevo León; no additional information was presented.

Recent collections that substantiate the distribution for *Pinus culminicola* are cited below: MEXICO, Coahuila, Mcpo. Arteaga, Sierra de Santa Maria E and S of La Ciruela, 12 Feb 1974, *Patterson 1102* (TEX); Sierra San Antonio, 5 km N of San Antonio de las Alazanas, 8 Oct 1974, *Patterson 32, 33* (TEX); head of Cañon San Antonio de las Alazanas between Sierra San Antonio and Sierra San Antonio de las Alazanas 7.5 km ENE of San Antonio de las Alazanas, 9 Oct 1974, *Patterson 36* (TEX). Nuevo León, Mcpo. Rayones, Sierra de la Marta, 21 Aug 1970, *Capó-Arteaga and Villarreal C. s.n.* (UNL).

The Coahuila-Nuevo León boundary falls along the Sierra de la Marta (also known as S. Santa Marta) axis but Mexican maps vary considerably in the placement of the state boundary. Both the Sierra de la Marta and the Sierra de San Antonio reach elevations in excess of 3400 m and are of a dolomitic limestone bedrock (at least in the upper portions). In addition, both sierras trend east-west and have extensive sheltered north exposures that rise steeply from a 2400 m base elevation. Sierra de la Marta is approximately 25° 13' N, 100° 23' W; Sierra San Antonio is 25° 17' N, 100° 38' W (fig. 1).

All of the Potosí piñon that we observed is restricted to open rocky sites at high elevations (above 3000 m) in sheltered sites usually but not exclusively on northern exposures. Such sites as the open summits of scarp faces or along high altitude crests of sierras seem to be preferred, e.g., on the Sierra de la Marta. We have also observed *P. culminicola* on shallow rocky soils in open sites within a mixed-conifer forest (S. de la Marta) as well as on open, rocky sites in mixed-conifer parklands (S. de San Antonio). In addition, *P. culminicola* is peripherally associated with an aspect of a high elevation (3000 m +) depauperate, open montane chaparral (sensu Muller, Amer. Midl. Naturalist 21:701-703, 1938) with low, gnarled, deciduous and evergreen scrub oaks, a variety of rosaceous and rhamnaceous shrubs and an *Agave* as the dominant associates (see *Patterson 36*).

In favorable habitats on the Sierra de la Marta, *P. culminicola* is frequently associated with a *Pinus-Pseudotsuga-Abies* community whose dominant species include *Pinus hartwegii*, *Pinus strobiformis*, *Pseudotsuga flahaultii*, and *Abies vejarii* (includ-